

2.2. Fire regimes after the arrival of Euroamericans

The arrival of Euroamericans in the Intermountain West brought far-reaching changes in land use and disturbance regimes. Agricultural burning, sparks from trains, and carelessness may have initially increased the frequency of fires. On the other hand, livestock grazing decreased the amount and continuity of fine fuel and therefore tended to decrease fire frequency. The drastic reduction in the area influenced by traditional Native American lifestyles probably also contributed to a reduction in fire frequency. Finally, the suppression of fires in accessible habitats also decreased fire frequency (Gruell 1983). It is doubtful that fire suppression would have been effective in the steeper canyons, however.

Little information is available on the fire regimes of northern intermountain steppe vegetation before the arrival of Euroamericans. Similarly, we know little about how often Native Americans set fire to intermountain grasslands. Dry coniferous forests experienced frequent low-intensity fires, many of which resulted from human activities. It is likely that some of these natural and anthropogenic fires also burned steppe vegetation, but the frequency and timing of those fires are not known. Soon after Euroamericans arrived in the region, fires may have become more frequent, but eventually fire suppression in uplands and the cessation of burning by Native Americans probably reduced the frequency of fire at moderate elevations. It is unlikely that fire suppression was effective in steep canyons.

3. Effects of burning on northern intermountain steppe

3.1. Effects of burning on vascular plants

3.1.1. Perennials

The responses of plants to fire depend upon species, weather, and fuel accumulations, as well as timing, intensity, and frequency of burning. The large number of relevant variables is one reason for apparent inconsistencies in the scientific literature on the effects of fire. To complicate matters, the parameters that are measured do not necessarily reflect the conditions experienced by burned plants. For instance, because the soil surface is typically darker and warmer on burned sites than on unburned sites, the former are generally phenologically advanced in comparison to unburned sites. Yet this is rarely taken into consideration when burned and unburned “controls” are compared (Daubenmire 1968a). Similarly, studies of the effects of fire intensity often report ambient temperature, but it is the temperatures of burning plant tissue that are ecologically important (Wright and Bailey 1982).

In steppe associations, Idaho fescue and needle-and-thread (*Hesperostipa comata*, formerly *Stipa comata*) tend to be damaged by fire and to recover relatively slowly, whereas damage to bluebunch wheatgrass, Sandberg bluegrass (*Poa secunda*), and prairie junegrass (*Koeleria macrantha*, formerly *Koeleria cristata*) is often relatively slight, and these species may be

stimulated after burning (Daubenmire 1975; Tisdale 1986; Johnson and Simon 1987; Johnson 1998). Similar differences in susceptibility have been observed in shrub steppe vegetation (Blaisdell 1953; Pechanec et al. 1954; Moomaw 1956; Mueggler and Blaisdell 1958; Wright and Klemmedson 1965; Conrad and Poulton 1966; Harniss and Murray 1973; Uresk et al. 1976, 1980; Nimir and Payne 1978; Clifton 1981; Kuntz 1982). (See Wright et al., 1979 and <http://www.fs.fed.us/database/feis/plants/graminoid/> for reviews.)

Bunchgrasses grow in compact tufts of densely clustered culms. Their meristematic tissue is in the form of buds located near the soil surface, and new growth is produced by the formation of new lateral shoots, or tillers, rather than by rhizomes. Since they lack rhizomes, caespitose grasses reproduce from seeds. These traits make them particularly vulnerable to damage from fire. Their densely clustered culms and leaves create compact bundles of fuel that may smolder for hours, and the resulting prolonged exposure to heat can damage plant tissue (Conrad and Poulton 1966).

Steppe vegetation generally burns at lower temperatures than vegetation dominated by shrubs or trees (Bailey and Anderson 1980). Bunchgrasses that have spreading leaves are less likely to be damaged by fire than species that form compact clumps. Because open clumps burn quickly, little heat is transferred to the soil surface, and the basal meristems of species with loose clumps are likely to survive. Bluebunch wheatgrass, which has an open growth form, is less likely to be harmed by fire than Idaho fescue, which has compact tufts that are severely damaged by burning (Conrad and Poulton 1966). In experiments in which Idaho fescue and bluebunch wheatgrass plants were burned at controlled temperatures, Idaho fescue plants subsequently developed damaged leaves, presumably because of destruction of meristematic tissue, but bluebunch wheatgrass did not (Defossé and Robberecht 1996). In addition, bluebunch wheatgrass buds are located slightly below ground level, which gives them some protection from fire (Antos et al. 1983).

Similarly, bottlebrush squirreltail (*Elymus elymoides*, formerly *Sitanion hystrix*) has features that make it resistant to fire, whereas the characteristics of needle-and-thread make it vulnerable to fire. Squirreltail tussocks have low density and burn quickly. Needle-and-thread forms denser bunches, which burn at higher temperatures and continue to burn long after a passing fire ignites the outer leaves. As a result, needle-and-thread plants are likely to be killed by fire, but meristematic crown tissue of burned squirreltail plants generally survives (Wright 1971; Young and Miller 1985).

It has also been suggested that grass clumps which have become elevated or “pedestaled,” either because of overgrazing or age, are particularly vulnerable to fire because their roots are exposed. This phenomenon has been reported in Sandberg bluegrass (Young 1943; Wright and Klemmedson 1965; Clifton 1981).

The position of seeds and buds and the amount of moisture they contain likewise influence susceptibility to fire. In general, the higher these organs are, the more likely they are to be damaged. Plants that burn before seeds have been shed suffer more damage than plants that have dropped their seeds, because seeds that are held aloft are exposed to more intense heat.

Seeds that are beneath a layer of litter are less likely to be damaged than seeds exposed on bare ground, and seeds lying on the soil surface are more vulnerable than seeds that are partially buried (Daubenmire 1968a). Managers can take advantage of this fact to burn exotic species when their seeds will be most vulnerable. For instance, burning medusahead (*Taeniatherum caput-medusae*) while seeds are still in the head is more effective than burning plants that have dropped their seeds (McKell et al. 1962).

Like perennial bunchgrasses, the forbs and dwarf shrubs of steppe and meadow steppe respond to fire in various ways depending on their growth form and phenology. Forbs that are able to regenerate from underground organs are usually not harmed by fire. Those with buds or rhizomes below the mineral soil surface or with taproots that can regenerate from below their crowns are most resistant to fire, especially if it occurs during the summer drought (McLean 1969; Antos et al. 1983). For example, arrowleaf balsamroot (*Balsamorhiza sagittata*) has a deep taproot (Figure 3) and often increases after burning, although repeated fires can cause severe crown injury that nevertheless prevents regeneration (Young 1943; Johnson 1998). Rhizomatous forbs generally increase after burning, whereas woody-based (suffrutescent) forbs are slow to recover (Blaisdell 1953). Daubenmire noted an instance in which prairie star (*Lithophragma*) increased after a fire swept through a bluebunch wheatgrass–Idaho fescue stand the preceding fall, and attributed this to dormant bulbils or seeds in the soil “that are far more abundant in virgin grassland than would appear from the normal populations” (Daubenmire, unpublished notes for steppe stand no. 41, Gooseneck Ridge, available at Washington State University Library, Manuscript, Archives, and Special Collections).

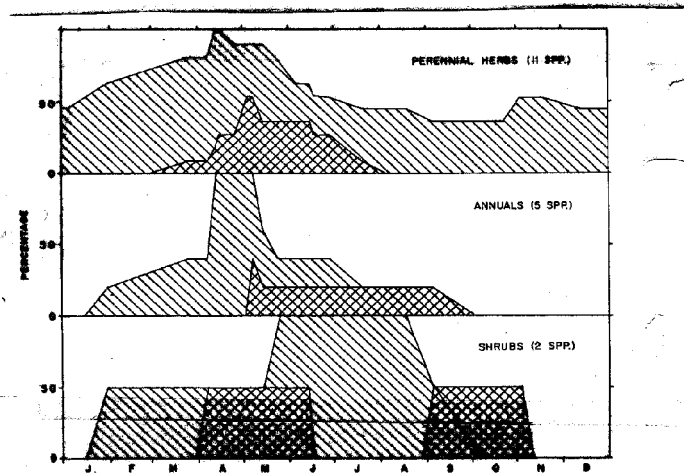
In general, burning favors herbaceous vegetation at the expense of trees and shrubs (Vogl 1974), but there is little evidence that fire limits the distribution of shrub or trees in steppe and shrub steppe. This is not surprising since snowberry and other low shrubs of meadow steppe resprout readily from rhizomes and return to their prefire state within three years (Daubenmire 1970; Kinateder 1998), and limited soil moisture in summer prevents trees from becoming established in this zone even in the absence of fire (Daubenmire 1968b).

In shrub steppe associations, the major shrubs are killed by fire, and responses to fire are influenced by loss of the sagebrush overstory. The death of the overstory dominants releases resources for grasses and forbs on burned shrub steppe sites, whereas this is not the case in true steppe or meadow steppe. For this reason, the contrast between the prefire and postfire environments is far greater in shrub steppe than in steppe, and comparisons between responses to fire in these two types of vegetation should be made with care.

Phenology also affects vulnerability to fire. Seasonal activity patterns are especially important in the intermountain region, where moisture and temperature do not peak at the same time. Because moisture is available during the cooler months, many steppe plants are dormant in summer but photosynthetically active from autumn through spring (Daubenmire 1972). This was noticed by early botanists who visited the region. Geyer remarked that native grasses renewed their growth “about the middle of September, during a series of wet, foggy cloudy days,” and even after the first frosts they continued to “grow a little” (Geyer 1846:287 footnote). Daubenmire estimated that about half the perennial herbaceous species in the bluebunch

wheatgrass-Sandberg bluegrass association and one third of the species of perennial herbs in the Idaho fescue/common snowberry association produce new foliage at the beginning of the rainy season and remain photosynthetically active throughout the winter (Daubenmire 1970) (Figure 4).

(A)



(B)

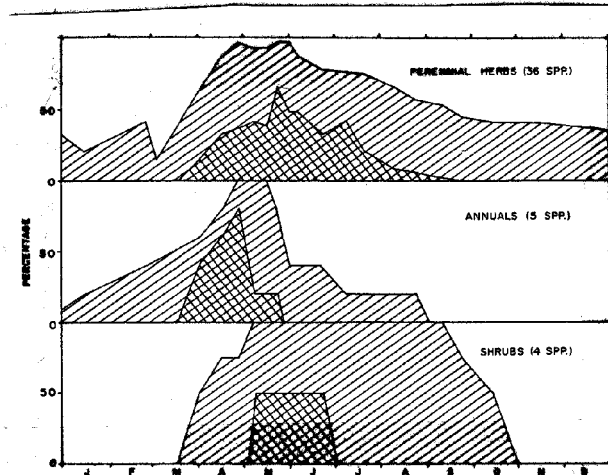


Figure 4. Phenology of native herbaceous species in an Idaho fescue/common snowberry association (A) and a bluebunch wheatgrass-Sandberg bluegrass association (B) in eastern Washington. Diagonal lines = actively growing; cross-hatching = pollinating. (After Daubenmire 1970.)

Burning is most damaging if it is conducted when plants are metabolically active. In regions with summer drought, this means that burning during the cool season entails a risk of damaging native perennials. Caespitose grasses typically produce tillers after the summer resting period. For example, bluebunch wheatgrass resumes growth slightly before rain moistens the soil of the root zone (Daubenmire 1972). Tillers become visible several weeks later and produce two or three fully expanded leaves by winter (Mueller and Richards 1986). These tissues are vulnerable to fires in autumn, winter, and spring, when they are photosynthetically active. The phenology of Idaho fescue is particularly advanced in comparison to other perennial grasses (Borman et al. 1990), which makes it especially vulnerable to early spring burning.

The annual cycles of a plant's energy reserves also affect its susceptibility to fire. It has been suggested that burning is especially detrimental if it occurs when carbohydrate reserves in underground storage organs have been depleted to produce foliage or fruits (Wright and Klemmedson 1965; Daubenmire 1968a; Beardall and Sylvester 1976).

Most natural burns of intermountain steppe vegetation would have occurred in mid or late summer, when the vegetation contained little moisture and lightning strikes were likely. We would expect native plants that evolved under this disturbance regime to have adaptations allowing them to survive late summer fires, and in fact they do. Most herbaceous plants are dormant at this time, so their aboveground tissues are not damaged by burning, and they regenerate readily from underground organs. For these reasons, late summer fires cause minimal damage to many native species (Daubenmire 1968a).

Native Americans were more likely to set fires in spring and fall than in summer, however. It is not clear to what extent these intentional burns had selected for adaptations to spring and fall burning.

3.1.2. Annuals

Annual forbs and grasses increase following fire if sufficient seeds survive or if a source of seeds is nearby. A few of these increasers, such as tall annual willowweed (*Epilobium brachycarpum*, formerly *paniculatum*), are native, but most are not. When livestock grazing and agriculture increased the frequency and the size of disturbances in the intermountain region, these changes favored European annuals such as cheatgrass or downy brome (*Bromus tectorum*), which had evolved with agriculture and livestock grazing (Mack 1981, 1986, 1988). The native grasses, on the other hand, were not well adapted to the new disturbance regime because they had never evolved adaptations to large-scale grazing and trampling. Although some large ungulates are native to intermountain steppes, huge herds of massive grazing mammals never roamed the region, so the dominant grasses did not evolve under the kind of grazing pressure that guided the evolution of steppe grasses exposed to bison herds in the Great Plains. The exotic species that were accidentally or deliberately introduced from Eurasia, however, had evolved with frequent and widespread disturbances and were able to exploit the newly disturbed environments (Tisdale 1961, Daubenmire 1970, Mack and Thompson 1982, Mack 1986).

Initially, cheatgrass colonized only sites that had been disturbed by grazing, farming, fires, or

other events that removed native vegetation, but eventually cheatgrass became so ubiquitous that it was even able to invade relatively pristine sites (Mack 1986; Brandt and Rickard 1994). Once established, cheatgrass affects native species unfavorably by successfully competing with them for moisture (Melgoza et al. 1990).

More recently, other alien annual grasses, such as medusahead (Torell et al. 1961), and forbs, such as yellow star-thistle (*Centaurea solstitialis*), have become serious problems (Kiemnec and McInnis 1994) in intermountain steppes. These exotics have the potential to increase flame lengths (Dick Walker, personal communications, January 26 and 31, 2001) and to alter fire frequency and intensity.

3.1.3. Rare plants

Over a dozen rare plant taxa, many of them endemics, occur in the northern intermountain steppes (Hill 1995*a,b*, 1996, Hill and Gray 1998*a,b*; Weddell and Lichthardt 1998). Like other plants of the region, these species evolved under the selective pressures exerted by the historical fire regime. The specific effects of fire on their demography are not well understood, however.

One species of particular concern is Spalding's catchfly, *Silene spaldingii*, a perennial forb that has been proposed for listing as federally threatened (Federal Register 64(232), December 3, 1999). In the Tobacco Plains of northwest Montana, at a site dominated by Idaho fescue and rough fescue (*Festuca altaica* ssp. *scabrella*, formerly *Festuca scabrella*), burning was followed by enhanced Spalding's catchfly recruitment (Lesica 1999). This effect was more pronounced with spring burning than with fall burning and was attributed to the removal of litter and creation of safe sites for germination. Fire might not have similar results in steppe habitats to the west of that study, however. The Tobacco Plains site is transitional between intermountain steppes and the steppes of the northern Great Plains, a region which is ecologically quite different from the intermountain region. Rough fescue is a coarse grass that produces "thick mats of persistent sheaths and culms bases" (Hitchcock et al. 1994:587), which create large amounts of litter that decomposes slowly. For these reasons, burning might have quite different effects on Spalding's catchfly populations east and west of the Rocky Mountains.

3.2. Effects of burning on microbiotic crusts

Many investigators have reported that in arid and semiarid environments burning decreases the biomass and cover of microbiotic crusts and alters their species composition (Countryman and Cornelius 1957; Antos et al. 1983; Schulten 1985; West and Hassan 1985; Johansen et al. 1984, 1993; Johansen and St. Clair 1986; Kaltenecker and Wicklow-Howard 1994; Johnson 1998; Youtie et al. 1999). (See Johansen and Rayburn 1989, West 1990, and St. Clair et al. 1993 for reviews.) On sites dominated by Idaho fescue, mosses and lichens located beneath bunchgrass tufts have especially high mortality (Johnson 1998), perhaps because of the high temperatures generated in the compact crown of this species. (See Section 3.1.1.) Soil algae typically recover after several years, but the recovery of mosses and lichens may take decades or centuries (Belnap 1993). Since the microbiotic crust affects soil texture and infiltration, nitrogen fixation, carbon cycling, plant nutrient status, and seedling establishment, its destruction has far-reaching

consequences (Evans and Johansen 1999). Aggregations of dead crustal material persist initially, but eventually they disintegrate, exposing the soil surface to wind and water erosion and to weed invasion (Johansen and Rayburn 1989). In addition, nutrient and hydrological cycles are altered.

3.3. Effects of burning on plant community composition

In forested landscapes, where light is a limiting factor, fire sets back succession, creating openings that can be colonized by pioneer species of seral communities. There is little evidence for fire-maintained species or communities in intermountain steppes, however. Neither Daubenmire (1970) nor Tisdale (1986) felt that historic fires had been a major force determining the composition or distribution of steppe communities in eastern Washington and west-central Idaho. Burning certainly favors some species over others and creates openings that can be exploited by pioneer species, but before the arrival of exotic grasses and forbs from Eurasia, the increases in ruderal species that followed burning probably lasted only a few years.

Burning decreases litter, and this can increase opportunities for seedling establishment. (See Section 3.1.3.) This effect is short-lived where annuals invade burned sites, however. In northeastern Oregon, burning decreased litter initially, but within a few years litter exceeded preburn levels because of the additional biomass contributed by annuals (Johnson 1998).

Native perennial bunchgrasses are susceptible to damage by fire because their meristematic tissues are exposed near ground level, they grow by means of tillers rather than rhizomes, and they reproduce by seeds. In addition, species that form very compact tufts and are phenologically advanced are especially susceptible. Idaho fescue has all of these characteristics.

Perennial forbs and shrubs that are able to regenerate from underground storage organs usually recover from burning. Native perennials are least vulnerable to fire when they are dormant, in summer. This is when most naturally started fires would have occurred in the past.

There is evidence that seedling recruitment in the rare Spalding's catchfly increases when communities dominated by rough fescue are burned. This is thought to be due to the removal of litter by fire. In intermountain steppes, where less litter is produced, it is less likely that litter limits recruitment.

Fire damages microbiotic crusts, and the recovery of crusts after burning may take years or even centuries. Annuals increase after fires if enough seeds survive to repopulate a site or if they can colonize it. Before the arrival of Eurasian annuals with superior adaptations for colonizing disturbed sites, these postfire changes in community composition were transient, but this is no longer the case.

4. Exotic species and changing fire regimes

As early as 1932, Pickford noted a positive feedback between fire frequency and cheatgrass invasion: "On promiscuously burned areas which have long been protected from grazing . . . burning tends to deplete the stand of perennial grasses and to allow annual grasses, chiefly downy brome, to increase sharply in density" (Pickford 1932:171). In addition to displacing

native species and causing a decline in forage quality, this shift in species composition has another serious consequence: cheatgrass increases the fire hazard because it provides large amounts of fine, highly flammable fuel. This in turn favors cheatgrass and other fire-adapted species (Peters and Bunting 1994). The destruction of the microbiotic crust by fire also favors disturbance-adapted species. In a cultivated field that was abandoned in 1920 and subsequently burned, cheatgrass became dominant by the second postfire season and remained so for at least 52 years (Daubenmire 1975).

The ubiquity of Eurasian annuals with superior ability to exploit disturbed areas has changed the consequences of fire in intermountain steppes. Cheatgrass and other alien annuals increase the supply of fine fuels, thereby increasing the likelihood of fires, a change which further favors annual exotics. Fire now “alters the biotic and abiotic factors enough that the plant community crosses a threshold from a perennial-dominated to an annual-dominated community” (Tausch et al. 1995:252).

After cheatgrass colonizes burned sites, it increases the supply of fine fuel, which promotes additional fires and leads to further increases in non-native species at the expense of natives.

5. Conclusions

Fire has effects at many levels of organization. After reviewing the effects of prescribed burning on an endangered forb of wetland prairies in the Willamette Valley, Pendergrass et al. (1999:1420) concluded that “the consequences of reintroducing burning must be considered at all ecosystem levels. A fire regime that is beneficial at one level of organization may be neutral or even detrimental at other scales, and managers need to be aware that potential benefits for one species or community may disadvantage others.”

Although restoring natural disturbance regimes is generally considered desirable, exotic species complicate the picture. Because species vary in their responses to burning, fires favor some species over others. Where aggressive, disturbance-adapted exotic species are present, fire can promote their establishment (Christensen and Burrows 1986; Hobbs and Huenneke 1992), and once invading species become established they may alter many properties of ecosystems, including their disturbance regimes (Vitousek 1990; D’Antonio and Vitousek 1992). In some cases, changes in species composition following fire lead to irreversible changes that prevent a return to the predisturbance community. This scenario differs from conventional models of succession, in which fire sets back succession and is followed by a predictable sequence of stages culminating in the re-establishment of a climax community. Rather, the introduced species create a new stable state. This appears to be the case when cheatgrass comes to dominate intermountain steppes (Tausch et al. 1993, 1995).

These circumstances create a dilemma for managers of intermountain steppes. Attempts to restore a natural ecosystem process to the landscape through prescribed burning may have

unintended consequences. Given the ubiquity of exotic annual forbs and grasses, fire is likely to favor the spread of non-native species at the expense of natives. This means that managers must decide which species they wish to manage for, and consider carefully the consequences of increasing the level of disturbance in an environment within which exotics are poised to take advantage of disturbance (Fox and Fox 1986), especially if populations of rare taxa could be harmed by the encroachment of annuals.

Efforts to restore fire to northern intermountain steppes should be evaluated carefully, for two reasons. First, it is not clear that the intermountain steppes have suffered dramatic negative consequences as a result of a change in fire frequency. While it seems likely that fires now occur less often than they did prior to the arrival of Euroamericans, we do not know the magnitude of that change in frequency or its consequences. Second, the benefits of burning are equivocal. There are some situations where the removal of accumulated litter may benefit native plants, but these benefits must be weighed against the risk that increases in exotic annuals will lead to irreversible losses of native vegetation.

The fire ecology of intermountain steppe is influenced by its distinctive physiognomy and phenology. Although dry forests were negatively impacted by fire suppression, the evidence for a similar situation in steppe communities, which have much lower fuel loads, is less compelling. Furthermore, burned stands of native steppe vegetation are vulnerable to invasion by cheatgrass and other annual exotics, an event which can irreversibly alter community composition.

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